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Variation in plumage, molt, and morphology of the Whiskered Auklet (Aethia pygmaea) in Alaska

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Abstract -- We studied molt and size variation in Whiskered Auklets collected at sea in August from the Aleutian Islands in 1992 and 1993. We evaluated size differences from external and skeletal measurements. Adults were molting extensively in August, indicating that molt began in July. Primaries 1-5 had been completely replaced, while primaries 6-8 were in various stages of replacement and primaries 9 and 10 were old in most birds. We also found that juveniles were not molting. This pattern is similar to other species of small auklets where breeding and molt in adults overlap, but juveniles do not molt until the following summer. This suggests that Whiskered Auklets are subjected to similar ecological constraints as other auklets. . We provide the first skeletal measurements of Whiskered Auklets and some new external measurements. Results of statistical analyses indicate that there is no sexual dimorphism in adults. A small sample of juveniles suggests that they are similar in size to adults.

Key words: auklet, Aleutians, seabird, Aethia pygmaea, molt, size, morphometrics

The Whiskered Auklet (Aethia pygmaea) is distributed among the Aleutian, Commander and Kuril islands of the northern Pacific Ocean and Bering Sea (Byrd and Williams 1993). Whiskered Auklets have been neglected in reviews of alcid life history and adaptive radiation (e.g. Storer 1945; Bédard 1969a; Sealy 1972) and many aspects of its biology are still poorly known (Byrd and Williams 1993, Gaston and Jones 1998). In their summary of the literature, Byrd and Williams (1993) noted that patterns of molt and plumages of Whiskered Auklets were poorly described and continue to be based mostly on early descriptions of Stejneger (1885), Bent (1919) and Dement'ev et al. (1951). Konyukhov et al. (in press) provide descriptions of the neossoptile, teleoptile plumages and fledglings in juvenile plumage. However, information on the timing of prebasic molt and its relation to breeding is still lacking. Overlap in the timing of molt and breeding differs among alcids (Sealy 1977, Bédard and Sealy 1984) and is probably related to body size, food availability and the energetic demands of breeding and molt (Foster 1975, Payne 1972). In this paper, we describe molt and plumage variation in Whiskered Auklets collected at sea from mid- to late August in the Aleutian Islands and compare these results with the pattern and timing of molt in other Alcids.

Information on intraspecific variation in body size is also lacking for this species. External measurements have been reported (Feinstein 1959, Byrd and Williams 1993) but there are no comparative analyses of males and females or of adults and juveniles using modern statistical methods. The evolution of sexual dimorphism in size has been associated with polygamous mating systems, intra-sexual selection for large size due to combat or predator defense, female choice and niche partitioning (Webster 1992). The presence or absence of sexual dimorphism could be important for understanding the evolution of feeding ecology, mating systems and courtship behavior of Whiskered Auklets. For example, there is evidence that sexual dimorphism in bill size and shape of a congener, the Crested Auklets (Aethia cristatella), is due to intra-sexual selection (Jones 1993). Finally, information on skeletal dimensions in the alcidae is rare but such information is useful for assessing sexual dimorphism (Piatt and Kitaysky 2002), geographic variation and genetic divergence in body size (Pitocchelli et al. 1995) and identifying remains from midden sites (e.g., Hobson and Driver 1989). Similar measurements are commonly used to identify beached marine birds and mammals (Ainley et al. 1994, Hass and Parrish 2000). Here we describe size variation among Whiskered Auklets using external measurements and present new data on skeletal measurements.

METHODS

Field work. We collected 56 specimens at sea near Egg Island (53˚ 20' N 166˚ 6' W) off the east coast of Unalaska Island, Aleutian Islands, Alaska from 10 – 25 August in 1992 and 1993. We examined plumage, molt and bill color and measured birds (see below) before preparing them in the field as skeletons for deposit in the American Museum of Natural History (New York, NY).

Color and plumage and analyses. Breeding adults have ornamental plumes on the head including a dark recurved frontal crest, white auricular plumes, and a white loral tuft with malar and superciliary branches (Stejneger 1885). We categorized four different groups of birds based on the presence and condition of ornamental plumes (Figure 1): 3 = dark recurved frontal crest, white auricular plume, white loral tuft with superciliary and malar branches (superciliary and malar branches of Stejneger 1885 are the superorbital and suborbital plumes respectively of Byrd and Williams 1993); 2 = lacks frontal crest and superciliary branches, possesses auricular plume, white loral tuft and malar branch; 1 = similar to 2 but lacks white loral tuft with some scattered white feathers at base of bill, 0 = no ornamental plumes but some white feathers at base of bill.

We recognized four categories of bill color: 0 = dark upper and lower mandibles; 1 = two-toned bills with dark upper mandible and lighter lower mandible; 2 = dull red upper and lower mandibles; 3 = bright red upper and lower mandibles with distinct black tip at the end of the bill. We noted iris color and foot color from fresh specimens prior to preparation as skeletons. All color determinations were made shortly after birds were collected and before post-mortem changes in color occurred.

We classified birds as juveniles or adults using a combination of criteria. Juveniles were not molting and had whisker scores of 0 and bill scores of 0 or 1. Adults were molting and had whisker scores of 1 - 3 and bill scores of 2, 3. Sex was determined by internal examination of reproductive organs.

We compared the stage of molt of primaries, secondaries and rectrices across sexes in adults and juveniles. We scored molting feathers following a protocol described in Emslie et al. (1990). For each of the 10 primaries, the percentage of growth was scored as follows: missing feather, less than 10% of the feather grown = pin feather, 10% growth, 30% growth, 50% growth, 70% growth, 90% growth, old feather or completely new feather. For primaries, we performed a frequency analysis of the number of adults with either old feathers, missing feathers, pin feathers, 10%, 30%, 50%, 70%, or 90% new feather growth. We performed separate analyses for males and females (Tables 1, 2). We also analyzed the number of birds molting secondaries and rectrices. All secondaries were lumped together and scored as old (all feathers were old), molting (some or all feathers were molting) or new (all feathers were new). We lumped rectrices together and applied the same molt scores: old, molting, new. Previous studies of other alcids (Sealy 1975, Bédard and Sealy 1984, Carter and Stein 1995) have shown that body molt was affected by breeding status (failed breeder versus successful breeder) but that primary molt was not. We assumed that this also applied to Whiskered Auklets but this deserves further study.

External measurements. Nares was measured from the middle of the anterior end of the nostril to the tip of the maxilla; gape as length of the bill from the gape from the corner of the mouth to the tip of the maxilla; bill depth as the height of the bill at the base; exposed culmen from the tip of the bill to the feathers of the forehead; flattened wing length to the neatest 1 mm using a wing rule; wingspan as the distance between the tips of the outstretched wings; tarsus from behind the midpoint of the joint of the tibia and metatarsus to the junction at the front of the metatarsus and base of the middle toe (see Baldwin et al. 1931). All measurements were taken to the nearest 0.01 mm with dial calipers. Weight (g) was measured with Pesola scales.

Skeletal Measurements. We measured (0.1 mm) 20 skeletal measurements (from Pitocchelli 1988, Robins and Schnell 1971,): PRL - premaxillary length, SKW - skull width, SKL - skull length, BDEP - bill depth, IN1W - proximal interorbital width, IN2W - distal interorbital width, MANDL - mandible length, CORL - coracoid length, SCAPL - scapula length, KEEL – keel length, KEED - keel depth, STERL – sternum length, SYNMAX - maximum synsacrum width, FEL - femur length, TIBL - tibiotarsus length, TARL - tarsometatarsus length, HUML - humerus length, RADL - radius length, ULNL - ulna length, CARPL - carpometacarpus length. Measurements were entered directly into computers using Max-cal digital calipers and Lessoft (Marcus 1982).

Morphometric analyses. We analyzed size measurements of males and females and of adults and juveniles from our collections. We computed elementary statistics for external and skeletal measurements of these groups using SPSS 6.1.1 for the Macintosh. We assessed sexual dimorphism in adults using a two-tailed Unpaired samples Student's t test. We performed separate Unpaired samples t tests on eight external and 20 skeletal measurements. We used the sequential Bonferroni test to adjust for the number of simultaneous tests and maintain a table-wide $\alpha = 0.05$ (Rice 1989).
We did not perform statistical tests on juveniles due to small sample sizes.

RESULTS

Color and plumage analyses. Foot color and iris color did not vary among 49 individuals. The feet were light blue, whereas the iris was creamy white. Plumage and bill color ranged between two extremes: 1) Adults in breeding plumage with bright red bills undergoing prebasic molt, to, 2) juveniles in juvenal plumage with dark bills, lacking ornamental plumes and not molting (Figure 1). Color of males or females did not differ, hence, we combined them for the analyses. Our frequency analysis of bill types (n = 49) revealed that 67.4% of the birds scored 2 or 3 (Figure 2A). Upper and lower mandibles of birds with scores of 2 and 3 varied from bright to dull red. Eight juveniles (16.3%) had completely dark bills (bill score = 0) while seven juveniles and one adult (16.3%) had two-toned bills (bill score = 1). Differences in bill color were probably due to bill molt. Peeling and shedding of the bill plates in these species results in a darker, grayish bill with remnants of red or orange from the breeding season. Changes in bill color and bill molt are initiated in August by Crested Auklets and Parakeet Auklets (Cyclorrhynchus psittacula) (Bédard and Sealy 1984).

Ornamental plumes of Whiskered Auklets are shorter in definitive basic plumage (Byrd and Williams 1993). Auklets from our sample (n = 49) were approximately evenly distributed among different categories of whisker scores for ornamental plumes (Figure 2B). Juveniles made up the largest group with score 0 followed by adults with score 3. The remaining birds were equally divided among groups with scores of 1 or 2 (Figure 2B). Molting of ornamental plumes among Whiskered Auklets is similar to that of Crested Auklets which undergo a prebasic molt of ornamental plumes in August (Bédard and Sealy 1984).

Primary molt in adult females was progressive, beginning with the innermost feathers and moving outward in ascending order (Table 1). P1 - P5 were new in all birds and most birds had replaced P6 (10 females, n = 18). Six of the remaining eight females showed either 70% or 90% new feather growth for P6 (Table 1). The number of females molting P7 varied the most; some birds had completely new feathers, whereas others were molting or had retained old feathers. Most females retained old feathers for P8 – P10 with the highest retention for P9 and P10. Secondaries and rectrices were molting in most females. None of the secondaries or rectrices had been completely replaced. Molt was similar in males (Table 2). P1 – P5 were new in all males and P6 was new for most males (10 males, n = 16). Like females, P9 and P10 were old feathers for most males and molt in P7 and P8 varied..

In contrast to adults, there was no evidence of prebasic molt in flight feathers of juvenile males or females. Primaries 1-10, secondaries and rectrices were new in juveniles of both sexes. Juveniles probably do not undergo a prebasic molt until the following summer, as in Crested, Least and Parakeet Auklets (Bédard and Sealy 1984). Juvenal plumage may provide enough thermal protection for the following year and precludes the need for an energetically expensive prebasic I molt in the fall (Bédard and Sealy 1984). Konyukhov et al. (in press) reported that the ornamental facial plumes and the frontal crest had developed to a varying extent in some juveniles at Buldir Island (western Aleutians) by the end of August, 1993. In some juveniles, ornamental plumes were as large as those of subadults. For reasons unknown to us, this differs from our birds in the eastern Aleutians where all juveniles lacked ornamental plumes and frontal crests.

Morphometric analyses. Table 3 contains elementary statistics for external and skeletal measurements of adult males and females, and juvenile males and females. External measurements were similar for males and females and across age groups. Males and females were also similar in size based on skeletal measurements (Table 3). There were no statistical differences between adult males and females (Table 3). We did not perform statistical tests on juveniles because of small samples.

DISCUSSION

Wing molt in Whiskered Auklets is progressive with primaries replaced from the innermost feathers outward in ascending order (Table 1, 2). The timing of wing molt strongly suggests that breeding and molt overlap. P1 – P8 from most birds in our samples had been replaced or were being replaced by late August. Egg laying, incubation, and brooding have been reported from July through the first week in August for populations in the Aleutian Islands (Byrd and Williams 1993). We assumed that auklets collected near Egg Island began molting in July and followed a breeding schedule similar to distant western populations. This pattern and timing of wing molt is like the progressive primary molt in Crested Auklets, Cassin's Auklets (Ptychoramphus aleutica) and Least Auklets (Aethia pusilla) where breeding and molt overlap (Storer 1960, Payne 1965, Bédard and Sealy 1984). Molt in these species differs from the synchronous molt of larger alcids, where the innermost primaries molt first— but outer feathers are lost before the inner primaries are fully grown— resulting in a period of flightlessness (Storer 1960, Payne 1965). Primary molt in Marbled Murrelets (Brachyramphus marmoratus) is similar to Whiskered Auklets where P1 – P6 are lost first, followed by the four outer primaries but they are flightless during this molt and molt does not overlap with breeding (Carter and Stein 1995).

Constraints of body size and foraging behavior may explain why some alcid species are able to molt during breeding. Small, planktivorous species like Cassin’s Auklets and the Aethia auklets , exploit energy-rich food resources that are superabundant during summer (e.g., oily crustaceans such as Thysanoessa euphausiids and calanoid copepods). Thus, food supplies may not restrict overlap of energetically demanding activities such as molt and breeding (Payne 1965, Bédard 1969b, Byrd and Williams 1993). In contrast, larger alcids that feed primarily on fish, such as Horned Puffins (Fratercula corniculata), Marbled Murrelets, Kittlitz's Murrelets (B. brevirostris), Ancient Murrelets (Synthilboramphus antiquus) may be more often limited by food supplies, and so have evolved to temporally separate molt and breeding activities (Payne 1972, Foster 1975, Sealy 1977, Bédard and Sealy 1984, Carter and Stein 1995). However, this argument is somewhat circular, trying to explain differences in biology between two groups on the basis of the fact that they are different.

There are some exceptions that help to support the hypothesis. Breeding and molt do not overlap in other planktivorous Alcids such as the Parakeet Auklet (Bédard and Sealy 1984) or Dovekie (Alle alle). However, the Parakeet Auklet does not typically rely on the dense, seasonal patches of crustacean plankton used by the Aethia auklets, rather it has a mixed diet that includes a lot of widely dispersed non-crustacean plankton (e.g., cephalopods and pteropods) (Bédard 1969b, Harrison 1990). Whereas the Dovekie (Alle alle) differs from Aethia and Ptychoramphus in having a synchronous molt, and breeding and molt do not overlap (Bédard 1985), it has a high-arctic distribution and a comparatively shorter breeding season which may impose greater constraints on energy budgets (Bédard 1985). Furthermore, the Dovekie is genetically distant from the Aethia auklets, having closest affinities with the fish-eating murres (Uria spp.) and Razorbill (Alca torda) (Friesen et al. 1996).

Based on weight, and external and skeletal measurements, Whiskered Auklets are the second smallest member of the Alcidae, slightly larger than Least Auklets (Byrd and Williams 1993). Byrd and Williams (1993) stated that male Whiskered Auklets were usually slightly larger than females in external measurements and mass, but qualified this by noting that they had small samples sizes for females (and in any case, did not conduct statistical tests of the data). We found no sexual dimorphism among adults in the external measurements considered by Byrd and Williams (culmen, wing, tarsus, mass), or other external and skeletal measurements we made. Our measurements suggests that juveniles differed from adults for some external measurements and body mass but skeletal measurements were very similar. However, our small sample sizes precluded statistical testing for differences between juveniles and adults.

In summary, Whiskered Auklets are morphologically and ecologically similar to other planktivorous Aethia auklets. Juveniles do not molt, and probably retain their juvenal plumage throughout the first summer. Adults undergo prebasic molt in mid- to late August. Bare parts such as the bill also change from breeding to winter colors in August, as observed in other auklets (Aethia, Cyclorrhynchus). Whiskered Auklets are monomorphic for overall body size.

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Table 1. Number of females molting primaries 1 – 10, secondaries and rectrices.

Feather	Old	Missing	Pin	10%	30%	50%	70%	90%	New
P1	0	0	0	0	0	0	0	0	18
P2	0	0	0	0	0	0	0	0	18
P3	0	0	0	0	0	0	0	0	18
P4	0	0	0	0	0	0	0	0	18
P5	0	0	0	0	0	0	0	0	18
P6	0	0	0	0	1	1	4	2	10
P7	1	0	0	3	2	1	3	3	5
P8	9	0	2	2	0	2	2	0	1
P9	17	0	0	0	0	0	0	1	0
P10	16	0	0	0	0	0	1	0	1
Secondaries	9			9 females with molting feathers					0
Tail	5			10 females with molting feathers					0

Table 2. Number of males molting primaries 1 – 10, secondaries and rectrices.

Feather	Old	Missing	Pin	10%	30%	50%	70%	90%	New
P1	0	0	0	0	0	0	0	0	16
P2	0	0	0	0	0	0	0	0	16
P3	0	0	0	0	0	0	0	0	16
P4	0	0	0	0	0	0	0	0	16
P5	0	0	0	0	0	0	0	0	16
P6	0	0	0	0	0	1	2	3	10
P7	1	0	1	2	3	2	0	1	6
P8	8	1	1	1	0	1	2	1	1
P9	9	0	2	2	1	2	0	0	0
P10	14	0	1	1	0	0	0	0	0
Secondaries	6			10 males with molting feathers					0
Tail	5			10 males with molting feathers					0

Table 3. Elementary statistics of external and skeletal measurements[1] of Whiskered Auklets (n and SD in parentheses for each group) and results of an Unpaired Samples Student's t test for adults with a correction using the sequential Bonferroni test.

Measurement	Adults		Significance	Juveniles	
	Males	Females	Level[2]	Males	Females
External Measurements					
Nares	5.02	5.11	ns	4.81	4.74
	(12, 0.39)	(18, 0.36)		(10, 0.36)	(5, 0.13)
Gape	19.94	19.87	ns	19.46	19.56
	(12, 0.55)	(18. 0.47)		(10, 0.87)	(5, 0.77)
Bill Depth	7.35	7.02	ns	6.50	6.32
	(12, 022)	(18, 0.37)		(10, 0.39)	(5, 0.13)
Culmen	10.16	10.14	ns	10.00	9.96
	(14, 0.39)	(18, 0.47)		(10, 0.79)	(5, 0.81)
Wing	108.56	109.83	ns	109.80	106.60
	(16, 4.90)	(18, 3.40)		(10, 2.49)	(5, 2.61)
Wingspan	37.62	37.16	ns	37.74	36.70
	(9, 0.50)	(10, 0.92)		(5, 0.70)	(4, 0.40)
Tarsus	21.84	21.62	ns	21.27	21.18
	(16, 1.45)	(18, 0.64)		(10, 0.81)	(5, 0.76)
Weight	117.35	114.72	ns	109.10	101.50
	(20, 9.12)	(18, 12.29)		(10, 8.24)	(4, 8.89)
Skeletal Measurements					
PRL	15.78	15.81	ns	15.97	14.94
	(19, 1.02)	(19, 1.11)		(9, 1.26)	(6, 1.23)
SKL	43.44	42.86	ns	42.62	42.01
	(18, 0.95)	(19, 0.88)		(8, 1.62)	(6, 1.19)

SKW	18.52	18.20	ns	17.87	17.86
	(19, 0.33)	(19, 0.41)		(6, 0.48)	(6, 0.81)
IN1W	4.98	4.79	ns	4.35	4.44
	(20, 0.28)	(19, 0.39)		(9, 0.33)	6, 0.59)
IN2W	2.58	2.45	ns	2.37	2.33
	(20, 0.23)	(19, 0.20)		(9, 0.19)	6, 0.32)
MANDL	30.97	30.51	ns	30.56	29.96
	(16, 0.68)	(18, 0.88)		(9, 1.07)	(5, 0.98)
BDEP	3.00	3.12	ns	3.26	2.83
	(20, 0.93)	(19, 1.16)		(9, 1.08)	(6, 1.19)
KEEL	60.22	59.04	ns	49.88	53.97
	(10, 1.98)	(16, 1.40)		(2, 2.74)	(3, 6.79)
KEED	20.61	20.64	ns	19.77	20.77
	(21, 0.73)	(19, 0.71)		(8, 1.14)	(5, 0.31)
STERL	54.59	53.52	ns	48.00	50.22
	(13, 1.42)	(16, 1.26)		(3, 4.85)	(2, 0.46)
CORL	19.61	19.41	ns	19.21	18.97
	(20, 0.58)	(18, 0.81)		(9, 0.84)	(6, 0.80)
SCAPL	33.14	33.00	ns	30.76	31.97
	(21, 1.21)	(18, 1.18)		(9, 1.67)	(5, 1.71)
SYNMAX	13.02	13.15	ns	12.24	12.84
	(21, 0.59)	(18, 0.53)		(9, 0.33)	(5, 0.43)
FEL	24.75	24.65	ns	24.63	23.75
	(19, 0.84)	(19, 0.59)		(8, 0.85)	(6, 0.24)
TIBL	42.23	42.65	ns	42.82	41.66
	(21, 1.87)	(18, 2.11)		(9, 2.46)	(5, 0.67)
TARL	20.54	20.55	ns	20.16	19.67
	(21, 1.02)	(19, 0.76)		(9, 1.04)	(6, 0.91)
HUML	36.93	36.81	ns	37.06	36.02

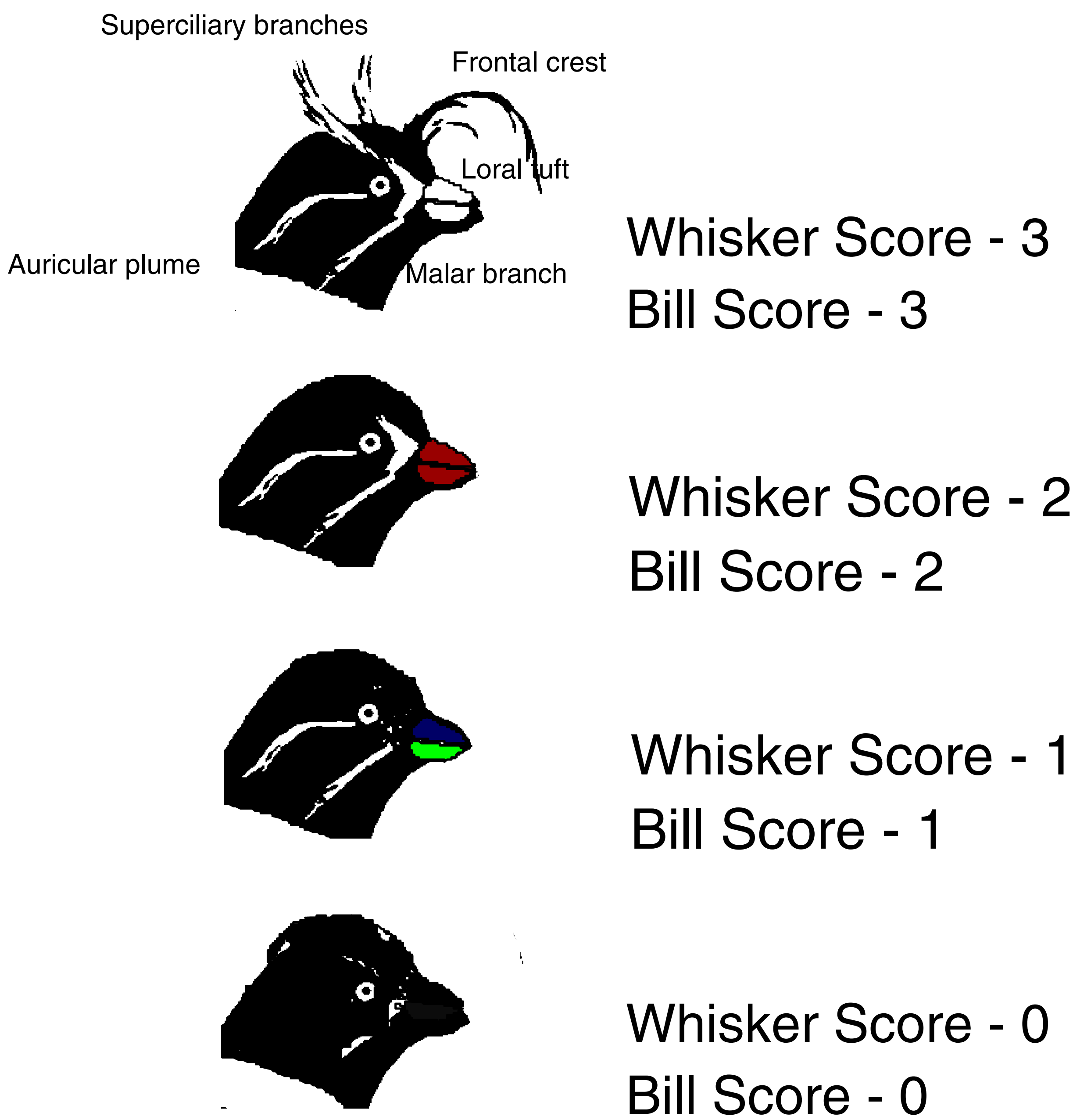
	(20, 1.17)	(17, 1.06)		(8, 1.38)	(6, 1.13)
RADL	30.82	30.86	ns	30.74	30.33
	(21, 0.99)	(19, 0.86)		(8, 0.57)	(6, 0.63)
ULNL	31.54	31.74	ns	31.47	31.13
	(19, 0.82)	(19, 0.89)		(8, 0.93)	(6, 0.75)
CARPL	20.65	20.74	ns	20.76	20.37
	(21, 0.89)	(18, 0.75)		(8, 1.08)	(6, 0.93)

[1] - size in mm and weight in g.

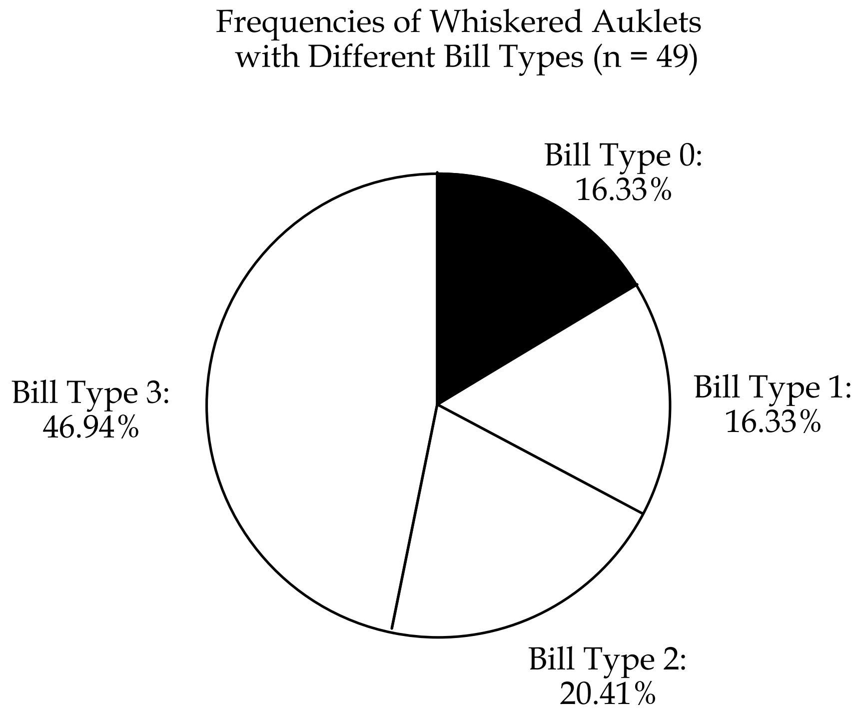
[2] – Unpaired Student's tests for adult males versus adult females, no tests were conducted on juveniles because of small samples.

Figure 1. Whisker and bill scores for Whiskered Auklets using terminology from Stejneger (1885). Superciliary and malar branches are equivalent to superorbital and suborbital plumes respectively of Byrd and Williams (1993).

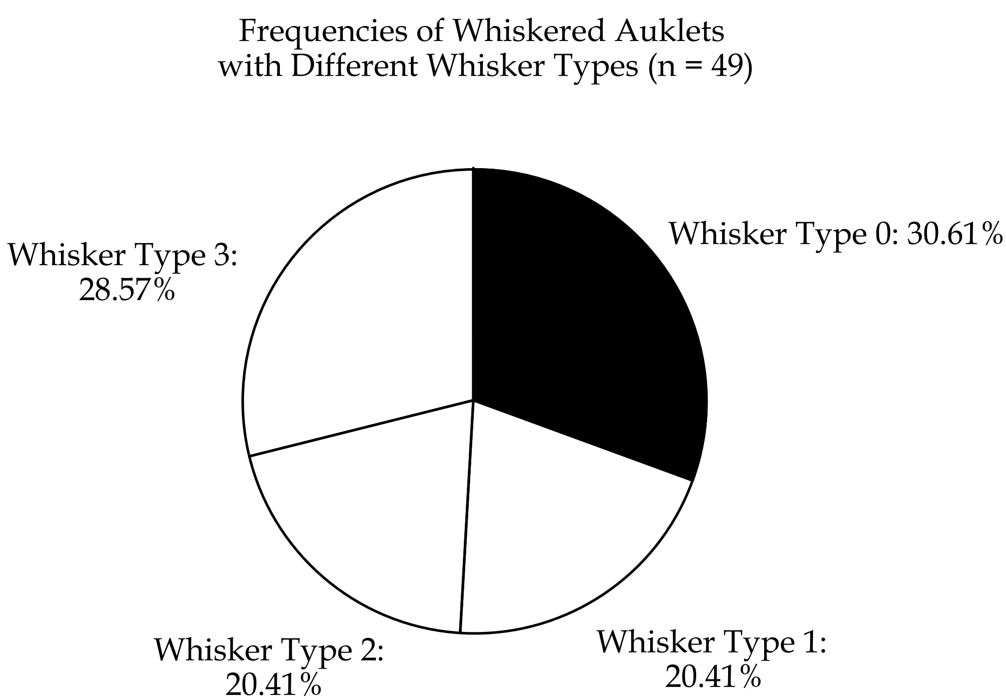
Figure 2. Frequency analysis of auklets with different bill and whisker scores. A - frequency of birds with different bill scores; B - frequency of birds with different whisker scores.


Superciliary branches
Frontal crest
Loral tuft
Auricular plume
Malar branch
Whisker Score - 3
Bill Score - 3
Whisker Score - 2
Bill Score - 2
Whisker Score - 1
Bill Score - 1
Whisker Score - 0
Bill Score - 0

A


Frequencies of Whiskered Auklets
with Different Bill Types (n = 49)
Bill Type 0:
16.33%
Bill Type 1:
16.33%
Bill Type 2:
20.41%
Bill Type 3:
46.94%

B


Frequencies of Whiskered Auklets
with Different Whisker Types (n = 49)
Whisker Type 0: 30.61%
Whisker Type 1:
20.41%
Whisker Type 2:
20.41%
Whisker Type 3:
28.57%